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PATTERNS OF PLANT INVASIONS AT SITES WITH RARE PLANT SPECIES THROUGHOUT NEW ENGLAND

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ABSTRACT. Although rare plant species are widely regarded as threatened by invasive plant species, few concrete data document the actual prevalence of invasives at sites with rare plant species. Data from comprehensive Conservation and Research Plans produced by the New England Wild Flower Society for 81 species of state-listed plants in New England provide quantitative information on the biogeographic distribution of invasive species where rare plants occur; their associations with multiple habitat variables and other threats; and hypothesized correlations with declines of rare plant populations. Eighteen invasive species were identified as co-occurring with rare plants; *Lythrum salicaria* was the most frequent and widespread. The spatial distribution of invasive species at rare plant sites paralleled large-scale patterns of both rare and invasive species richness and frequency throughout the region. However, invasive species occurred at only a subset of rare species sites, principally clustered along major rivers in New England. Connecticut reported the highest frequency and diversity of invasives, which declined with latitude. Invasives co-occurred with 38 (47%) of 81 rare species at 10.4% of 820 rare plant populations studied. For affected rare taxa, invasive species posed threats to a mean of 37.7% of their New England populations. Paired comparisons of invaded and uninvaded rare plant populations revealed a significant association of invasives with roads and with other anthropogenic threats. Populations of rare taxa in proximity to invasives showed higher (but statistically insignificant) rates of decline; classification analysis indicated that decline was best explained by the same habitat variables that were associated with invasive species presence, rather than by the presence of invasives alone. Thus, invasive species are both a direct threat and a symptom of larger landscape variables that influence the persistence of rare species.

Key Words: biogeography, invasive species, endangered plants, rarity, New England, conservation, invasibility

Invasive plant species are widely regarded as a significant threat to rare plant species, and may play a pivotal role in the endangerment of as many as half of all listed plants in the United States (Randall and Marinelli 1996; Westbrooks 1998; Wilcove et al. 1998). The general spatial distribution and impacts of invasive plant species in New England remain to be documented in detail (Farnsworth and Meyerson 1999a), although efforts are currently underway to identify invasives and to map their spread

(Mehrhoff et al. 2003). As yet, no data have been compiled specifically on the occurrence and effects of invasive plant species at sites with rare and listed plant species of the region. Concrete data are critical for understanding the scope and nature of invasions and for developing and justifying policies and management strategies to reduce their negative impacts on species of conservation concern. This paper analyzes detailed data on the presence and impacts of invasive species co-occurring with populations of 81 species of plants that are state-listed in one or more New England states. This data set has been collated from Conservation and Research Plans recently published by the New England Wild Flower Society, non-regulatory documents analogous in format and peer-review process to U.S. Fish and Wildlife Service Endangered Species Recovery Plans (Farnsworth 2003; New England Wild Flower Society 2003). Authors of plans collected these data from Natural Heritage Program Element Occurrence Records and their own observations of sites. These data provide a unique opportunity to:

1. map occurrences of invasive species, investigate biogeographic patterns, and pinpoint concentrations of invasions at particular types of sites where rare species occur;
2. identify which invasive species are most frequently impinging on rare species;
3. perform paired comparisons on invaded and uninvaded populations of rare plants to determine if invasions are associated with consistent environmental variables and/or with decline of rare plant populations; and
4. explore whether consistent differences exist among rare species for which invasive species are reported and those for which invasive species are not considered to be a threat.

MATERIALS AND METHODS

Data collection. The New England Plant Conservation Program (NEPCoP) of the New England Wild Flower Society initiated a five-year project in 1999 to complete comprehensive Conservation and Research Plans for 100 state-listed species. The species covered were chosen from over 300 taxa that were reviewed in the *Flora Conservanda* (Brumback and Mehrhoff, et al. 1996), and generally are listed as rare in one or more New England states. Each plan thoroughly reviews the taxonomy, ecology, biogeography, and conservation status of every known New England population of the rare taxon covered, and synthesizes the state of the knowledge about each taxon throughout its entire range. Each plan then develops a set of quantitative, prioritized objectives designed to ensure the taxon's viability in New England throughout the next twenty years, based on its current status, its apparent habitat requirements, and the feasibility of alleviating threats and protecting populations at extant and new localities. Each plan stipulates specific actions, including monitoring, protection activities, management, *ex situ* collection, and scientific studies, that will meet these objectives. Plans are subjected to three rounds of rigorous, extra- and intramural peer review, in which they are evaluated for accuracy, clarity, internal consistency, and feasibility (cf. criteria of Brigham et al. 2002; Hoekstra et al. 2002). To date, 80 such plans have been published, covering 81 species. In writing these plans, authors frequently visited sites of extant rare plant occurrences to update information on population numbers and threats, including the presence of invasive species. Where site visits were not possible, information was summarized from previously existing Element Occurrence Records from each state's Natural Heritage Program. The data documented in field forms have been compiled by professional botanists or trained volunteer monitors (usually working with the New England Plant Conservation Program) who have visited sites, quantified population sizes of the target rare taxa, and described threats to population viability including the presence of invasive plant taxa within close proximity. The data have been meticulously collected. Field forms are standardized and call for the same type and quality of data from state to state, and the field observations of *in situ* threats to rare species show strong concordance among years and observers (Farnsworth, unpubl. data). Field forms have been assessed carefully for consistency and quality-control prior to being entered into Natural Heritage or NEPCoP databases. The data also have been critically evaluated by authors and reviewers of the Conservation Plans. However, it must be acknowledged that any data taken by a range of observers will necessarily be subject to observational bias and variability among individuals.

Based on data compiled for each plan, the following variables were entered into a table containing information on all 81 species covered to date [rows corresponded to individual Element Occurrences (EOs)]: Species; Family; County; Town(s); Date of First Observation; Date of Latest Observation; Population Status (actual or estimated numbers of ramets or genets at each time of survey); Description of Habitat; and Threats to the Taxon at the Site. A list of the rare species included in the data set is given in Table 1. For the purposes of this analysis, confirmed historic and extirpated EOs were excluded (invasive species had not been

Table 1. List of 81 state-listed plant species included in the analysis. Species with one or more populations affected by invasive species are given in bold-face type. "Invasive Species" column number codes correspond to the invasive species (listed in Table 2) that were identified as associated with the corresponding rare species; numbers in brackets denote the number of extant populations affected by invasives/the total number of extant populations.

Species	Family	Invasive Species
Echinodorus tenellus **(Mart.) Buchenau**	**Alismataceae**	1 [1/1]
Taenidia integerrima **(L.) Drude**	**Apiaceae**	2,6,7,8,18 [7/10]
Zizia aptera **(A. Gray) Fernald**	**Apiaceae**	3,4,6,9 [2/3]
Aristolochia serpentaria **L.**	**Aristolochiaceae**	2,5 [2/12]
Asclepias purpurascens **L.**	**Asclepiadaceae**	3 [1/5]
Ageratina aromatica (L.) Spach	Asteraceae	[0/5]
Doellingeria infirma **(Michx.) Greene**	**Asteraceae**	2 [1/3]
Eupatorium leucolepis (DC.) Torr. & A. Gray var. *novae-angliae* Fernald	Asteraceae	[0/17]
Hasteola suaveolens **(L.) Pojark.**	**Asteraceae**	4,9 [1/1]
Hieracium robinsonii (Zahn) Fernald	Asteraceae	[0/1]
Liatris scariosa **Willd. var. *novae-angliae*** **Lunell**	**Asteraceae**	3,8,9 [6/77]
Nabalus serpentarius Pursh	Asteraceae	[0/10]
Polymnia canadensis **L.**	**Asteraceae**	10 [1/3]
Sclerolepis uniflora **(Walter) Britton, Sterns & Poggenb.**	**Asteraceae**	12 [1/2]
Solidago rigida **L.**	**Asteraceae**	3,6,8,9 [2/6]
Symphyotrichum concolor (L.) G.L. Nesom	Asteraceae	[0/6]
Cynoglossum virginianum L. var. *boreale* (Fernald) Cooperr.	Boraginaceae	[0/8]
Hackelia deflexa var. *americana* (A. Gray) Fernald & I.M. Johnst.	Boraginaceae	[0/19]
Neobeckia aquatica **(Eaton) Greene**	**Brassicaceae**	1,12,14 [2/4]
Moehringia macrophylla (Hook.) Fenzl	Caryophyllaceae	[0/16]
Paronychia argyrocoma (Michx.) Nutt.	Caryophyllaceae	[0/28]
Silene stellata **(L.) W.T. Aiton**	**Caryophyllaceae**	2,3 [1 /2]
Hypericum adpressum Barton	Clusiaceae	[0/14]
Carex atherodes Spreng.	Cyperaceae	[0/2]
Carex barrattii Schwein. & Torr.	Cyperaceae	[0/2]

Table 1. Continued.

Species	Family	Invasive Species
Carex davisii Schwein. & Torr.	**Cyperaceae**	2,3,5,6,7, 10,15 [5/8]
Carex garberi Fernald	Cyperaceae	[0/27]
Carex polymorpha Muhl.	Cyperaceae	[0/15]
Carex richardsonii R. Br.	Cyperaceae	[0/1]
Carex wiegandii Mack.	Cyperaceae	[0/34]
Cyperus houghtonii Torr.	Cyperaceae	[0/16]
Rhynchospora capillacea Torr.	**Cyperaceae**	1,4,8,11,15 [6/8]
Rhynchospora inundata (Oakes) Fernald	Cyperaceae	[0/10]
Rhynchospora nitens (Vahl) A. Gray	Cyperaceae	[0/13]
Schoenoplectus etuberculatus (Steud.) Sojak	**Cyperaceae**	4 [1/1]
Scirpus longii Fernald	**Cyperaceae**	1,4,7 [4/28]
Eriocaulon parkeri B.L. Rob.	**Eriocaulaceae**	1 [1/40]
Desmodium cuspidatum (Muhl.) Loudon	Fabaceae	[0/8]
Oxytropis campestris (L.) DC. var. *johannensis* Fernald	Fabaceae	[0/6]
Senna hebecarpa (Fernald) Irwin & Barneby	**Fabaceae**	5 [1/6]
Corydalis flavula (Raf.) DC.	**Fumariaceae**	5 [1/4]
Hydrophyllum canadense L.	**Hydrophyllaceae**	2,5,17 [3/5]
Juncus vaseyi Engelm.	Juncaceae	[0/6]
Agastache nepetoides (L.) Kuntze	Lamiacaeae	[0/2]
Agastache scrophulariifolia (Willd.) Kuntze	Lamiaceae	[0/4]
Scutellaria integrifolia L.	**Lamiaceae**	3 [1/ 2]
Chamaelirium luteum (L.) A. Gray	**Liliaceae**	5,6 [2/11]
Triantha glutinosa (Michx.) Baker	Liliaceae	[0/39]
Linum sulcatum Riddell	Linaceae	[0/2]
Diphasiastrum sitchense (Rupr.) Holub	Lycopodiaceae	[0/9]
Rotala ramosior (L.) Koehne	**Lythraceae**	1 [2/9]
Rhexia mariana L.	Melastomataceae	[0/9]
Pterospora andromedea Nutt.	**Monotropaceae**	7 [1/3]
Ludwigia polycarpa Short & Peter	**Onagraceae**	1,11 [2/10]
Ludwigia sphaerocarpa Elliott	**Onagraceae**	1,4 [2/6]
Botrychium lunaria (L.) Sw.	Ophioglossaceae	[0/4]
Amerorchis rotundifolia (Banks *ex* Pursh) Hultén	Orchidaceae	[0/7]
Goodyera oblongifolia Raf.	Orchidaceae	[0/13]
Listera auriculata Wiegand	Orchidaceae	[0/13]

Table 1. Continued.

Species	Family	Invasive Species
Listera australis Lindl.	Orchidaceae	[0/3]
Listera convallarioides (Sw.) Nutt.	Orchidaceae	[0/8]
Listera cordata **(L.) R. Br.**	**Orchidaceae**	1 [1/8]
Triphora trianthophora Rydb.	Orchidaceae	[0/23]
Oxalis violacea **L.**	**Oxalidaceae**	3,4 [2/16]
Panicum flexile (Gatt.) Scribn.	Poaceae	[0/2]
Sphenopholis nitida **(Biehler) Scribn.**	**Poaceae**	8 [1/9]
Polemonium vanbruntiae Britton	Polemoniaceae	[0/10]
Potamogeton ogdenii **Hellquist & Hilton**	**Potamogetonaceae**	12,14 [2/6]
Stuckenia filiformis (Pers.) Börner subsp. *occidentalis* (J.W. Robbins) R.R. Haynes, D.H. Les & M. Král	Potamogetonacae	[0/4]
Adiantum viridimontanum C.A. Paris	Pteridaceae	[0/7]
Hydrastis canadensis **L.**	**Ranunculaceae**	2,3,5,6,10 [3/7]
Ranunculus lapponicus L.	Ranunculaceae	[0/8]
Trollius laxus Salisb.	Ranunculaceae	[0/6]
Rosa acicularis **Lindl. subsp. *sayi*** **(Schwein.) W. H. Lewis**	**Rosaceae**	2 [1/5]
Populus heterophylla **L.**	**Salicaceae**	2,5 [1/7]
Saururus cernuus **L.**	**Saururaceae**	1 [1/3]
Castilleja coccinea **(L.) Spreng.**	**Scrophulariaceae**	1,5 [1/8]
Mimulus moschatus **Douglas**	**Scrophulariaceae**	2,13 [4/16]
Pedicularis lanceolata **Michx.**	**Scrophulariaceae**	1,4,7,16 [5/7]
Valeriana uliginosa **(Torr. & A. Gray) Rydb.**	**Valerianaceae**	4,13,15 [3/18]
Verbena simplex Lehm.	Verbenaceae	[0/3]

noted as the direct cause for any local extinction in the data set and verified, current information on extant populations was preferred). Also excluded were equivocal EOs for which invasive species were noted only as "nearby" or a "potential threat." Observers categorized invasive species as actual threats to rare taxa when strong evidence of direct competition (shading, physical smothering, etc.) was seen. The resulting data set contained 820 EOs. In a small proportion of cases (16%), sites were observed over several years, and the expansion of invasives or competitive exclusion of a rare species could be unambiguously documented. For this subset of populations for which unambiguous data were available, population decline (as a binary variable, decline or not) could be surmised from inspection of population levels at multiple sampling dates. For the majority of cases, however, these observations represent a static and necessarily qualitative assessment of the impacts of invasive plants on the rare taxon, gathered by trained botanists. To date, these are the only data available; long-term, experimental studies of interactions between invasive and rare plants have not been conducted in New England.

Data analysis. Taxa classified as "Invasive" or "Likely Invasive" by the Massachusetts Invasive Plant Working Group (2003) were used to delimit the list of invasive taxa examined in the plans; this list encompasses all of the most common species identified as invasive by Natural Heritage Programs and other botanists throughout New England. Species nomenclature follows this list; however, since not all authors distinguished individual species of bush honeysuckles (*Lonicera* spp.), these were grouped as a single taxon. Because precise coordinates do not exist for all EOs, and to preserve confidentiality of exact locality information, occurrences of invasive species at rare species sites were mapped at the town polygon level using Geographic Information Systems software (ArcView 3.2, ESRI, Redlands, CA). To compare distributions of invasive species at rare species sites with the overall biogeographic distribution of invasive species, data were pooled by county (the best resolution currently available) and compared to data from county-level maps published in Magee and Ahles (1999) showing the presence/absence of invasive species.

I tested the hypothesis that, within species, populations with one or more invasive species present would differ consistently from populations without invasive species reported in terms of the following variables:

1. Habitat type, 11 classes coded: land in agriculture; coastal plain pond; upland field; floodplain; lacustrine; outcrop/summit/talus; power line right-of-way; rich woods; acidic rocky woods; wetland (wet meadow; marsh; bog; swamp); railroad.
2. Other identified threats, 16 classes coded: agriculture; collection/harvesting; natural disturbance including flooding, tidal overwash, treefalls, etc.; trampling; vulnerability to drought; dumping; erosion; eutrophication; herbicide application; herbivory; alterations in hydrology; logging; mowing; road construction; natural succession; or none.
3. Proximity to roads: yes if within 100 m; no if farther away.
4. Site protection status: 1 if owned or managed by a conservation organization; 0 if not.

5. Evidence of decline among sampling years: yes; no (from the subset of cases with multi-year data on plant population size).

Additional landscape variables examined included: circumneutral soils (yes, no), proximity to foot trails (as with roads), and an index of light availability (1 = shade to 5 = full-sun habitats). However, none of these additional variables explained variance in the model, so only the five categorical variables listed above were used in the analysis.

For the subset of 37 species with both invaded and uninvaded sites, invaded EOs were paired with uninvaded EOs according to geographic proximity (i.e., EOs were paired with EOs of the same species occurring in the same town or county) to control for variability in environmental factors such as climate and underlying bedrock. Sign tests were performed on the above variables using SYSTAT 8.0 for Windows (SPSS Inc., Chicago, IL) to test the null hypothesis that each of the variables above would not differ consistently by invasion status.

Another data set was used to compare among rare plant taxa with one or more invaded populations (N = 38 species) with those that had no such threats reported at any site (N = 43 species). This unpaired comparison tested whether consistent differences in the above variables characterized invaded versus uninvaded taxa (using classification tree analysis and inspection of frequency tables). The above variables were coded as a single "archetypal" case that broadly characterized the EO, based on inspection of each EO and a tabulation of the status of the majority of cases. For example, if the majority of EOs occurred in close proximity to a road or were declining between observation dates, these variables were coded as 1. The most frequent habitat type and threats characteristic of the majority of EOs were also used. Likewise, I examined the number of populations now regarded as "historic" or "extirpated" for each species, as a proportion of all populations recorded since the species was first documented in New England, testing the hypothesis that species with invaded populations showed a higher frequency of population loss than uninvaded species.

Categorical classification tree analysis using a Gini Index fitting method was run in SYSTAT to model the dependence of the response variable ("invaded" yes or no for either populations within taxa, or among invaded and uninvaded taxa) on this suite of categorical variables. Similar models were constructed to investigate the dependence of the variable "decline" (yes or no) on invaded status and the above variables. Classification analysis is analogous to a dichotomous botanical key, in which taxa are split into groups based on morphological or other variables

(Gotelli and Ellison, 2004). It is a very useful method for analyzing data in which the explanatory variables (analogous to characters in a key) can be either categorical or numerical, or which contain missing values (De'ath and Fabricius 2000). Classification trees repeatedly split the data (in this case, distinguishing "invaded" and "uninvaded" cases) into smaller categories, where each split depends on a single variable. Each split results in two groups, one containing a majority of "invaded" cases, the other containing a majority of "uninvaded" cases. The splitting continues until no further improvement in the statistical fit of the model can be attained, and the endpoint is as homogeneous as possible (i.e., each terminus contains as close as possible to 100% of the "invaded" or the "uninvaded" cases). An impurity index (based on the Gini Index) can be calculated to describe the reliability with which the model distinguishes among the categories of cases. For example, if the splitting variables successfully separate all of the "invaded" cases from the "uninvaded" cases, an impurity index of zero results. Predictive capacity of the model decreases as the impurity index increases. A proportional reduction in error (PRE) score indicates the proportion of variance in the data explained by the model as a whole.

RESULTS

Thirty-eight (47%) of the 81 rare species studied had one or more invasive species present at one or more populations (Table 1). Eighty-five (10.4%) of 820 populations studied had one or more invasive species present. For the subset of rare plant species that co-occurred with invasives, invasives posed threats to a mean of 37.7% (±27%, SD) of populations. The species classified as "invaded" fell into 27 families (Table 1). Ten families (Boraginaceae, Clusiaceae, Juncaceae, Linaceae, Lycopodiaceae, Melastomataceae, Ophioglossaceae, Polemoniaceae, Pteridaceae, and Verbenaceae) had no rare species with invasive occurrences. Families with multiple species experiencing invasions included the Apiaceae, Asteraceae, Cyperaceae, Onagraceae, and Scrophulariaceae. Invasive species themselves hailed from 16 plant families, only six of which overlapped with the 37 total rare families recorded here (Lythraceae, Poaceae, Brassicaceae, Fabaceae, Asteraceae, and Apiaceae).

Eighteen invasive taxa were identified as occurring at rare species sites (Table 2), with 110 total instances tabulated. *Lythrum salicaria* (purple loosestrife) was both the most frequent invasive species mentioned at rare species sites (with 20 occurrences region-wide) and the most widespread

Table 2. Invasive taxa identified as occurring at rare species sites. Second column reports the total number of occurrences throughout New England. Numbers in the column under each state abbreviation indicate numbers of invasive occurrences reported.

Species	Total	CT	MA	VT	NH	ME	RI
1. *Lythrum salicaria* L.	20	6	8	3	1	2	
2. *Berberis thunbergii* DC.	14	3	7	4			
3. *Celastrus orbiculatus* Thunb.	10	7	3				
4. *Phragmites australis* (Cav.) Trin. *ex* Steud.	9	3	3			1	2
5. *Rosa multiflora* Thunb.	9	6	3				
6. *Lonicera* spp.	9	5		4			
7. *Rhamnus cathartica* L.	8		2	5	1		
8. *Cynanchum louiseae* Kartesz & Gandhi	6	4		1			1
9. *Elaeagnus umbellata* Thunb.	4	3					1
10. *Alliaria petiolata* (M. Bieb.) Cavara & Grande	4	2	1	1			
11. *Polygonum cuspidatum* Siebold & Zucc.	4		1	2	1		
12. *Myriophyllum spicatum* L.	3	1		1	1		
13. *Tussilago farfara* L.	3		1		1	1	
14. *Trapa natans* L.	2		1	1			
15. *Frangula alnus* P. Mill.	2	1				1	
16. *Microstegium vimineum* (Trin.) A. Camus	1	1					
17. *Aegopodium podagraria* L.	1			1			
18. *Robinia pseudoacacia* L.	1			1			
TOTAL SPECIES		12	10	11	5	4	3
TOTAL OCCURRENCES	110	42	30	24	5	5	4

species (occurring in 5 of 6 New England states). *Berberis thunbergii* (Japanese barberry), *Celastrus orbiculatus* (oriental bittersweet), *Phragmites australis* (common reed), and *Rosa multiflora* (multiflora rose) followed in frequency (Table 2). Obviously, these invasive species are more widespread in New England than the number of occurrences reported here; our focus here is restricted to sites from which both rare and invasive species are known to co-occur.

Connecticut reported the highest number of invasive species at rare plant sites overall, with 42 occurrences (and a total of 12 invasive species) noted statewide. Massachusetts was second, followed by Vermont, New Hampshire, Maine, and Rhode Island (Table 2). The frequency of invasive species occurrences at rare plant sites largely paralleled the longitudinal pattern of invasive species richness recorded in Magee and Ahles (1999), with concentrations of invasives in the southwestern and western regions of New England and richness declining from southwest to northeast (Figure 1). The number of invasive species occurrences per state at rare species sites was positively, but not significantly correlated with the mean number of invasive species reported per county by Magee and Ahles ($r^2 = 0.501$, but $P = 0.116$ due to a low sample size of 6 states). A positive correlation also existed between the number of invasive occurrences at rare species sites in a county and the number of rare species occurrences reported per county ($r^2 = 0.280$, $P = 0.005$), indicating that sites with high frequency and richness of rare species exhibited somewhat more frequent invasions.

Clusters of sites with rare plant species and co-occurring invasive species became evident when the data were mapped at the town level for New England (Figure 1). In large part, this distribution reflected "hot spots" of rare plant occurrences. However, invasive species occurred only at a subset of rare species sites across the region. Rare species co-occurred with invasive species particularly frequently along major water courses, including the Connecticut River, Housatonic River, and Lake Champlain; the St. John River in northern Maine also had an isolated invasive species report at a rare plant station. Rare and invasive species also tended to co-occur in regions of New England distinguished by circumneutral soils derived from alluvium and/or calcium-rich bedrock, particularly along the Stockbridge marble belt of western Connecticut, Massachusetts, and Vermont and traprock basalts of the Metacomet Range in west-central Massachusetts and Connecticut. Because rare plant species are less frequently found in proximity to dense population centers in New England, invasive species were not clustered around cities in this data set, even though their frequency in general tends to correlate positively with human population density.

For a subsample of 37 species with both invaded and uninvaded populations, paired comparisons were performed between neighboring populations with and without invasive species present (N = 63 site comparisons). Sign tests indicated that invaded populations were associated significantly and more frequently with nearby roads ($\chi^2 = 3.72$; df = 1, $P = 0.05$). Classification analysis yielded a model that separated invaded and uninvaded sites first by a suite of threats more frequently associated with invaded sites: dumping, hydrological alteration, eutrophication, trampling, herbicide use, succession, drought, erosion, and natural disturbance (Figure 2). For populations facing these

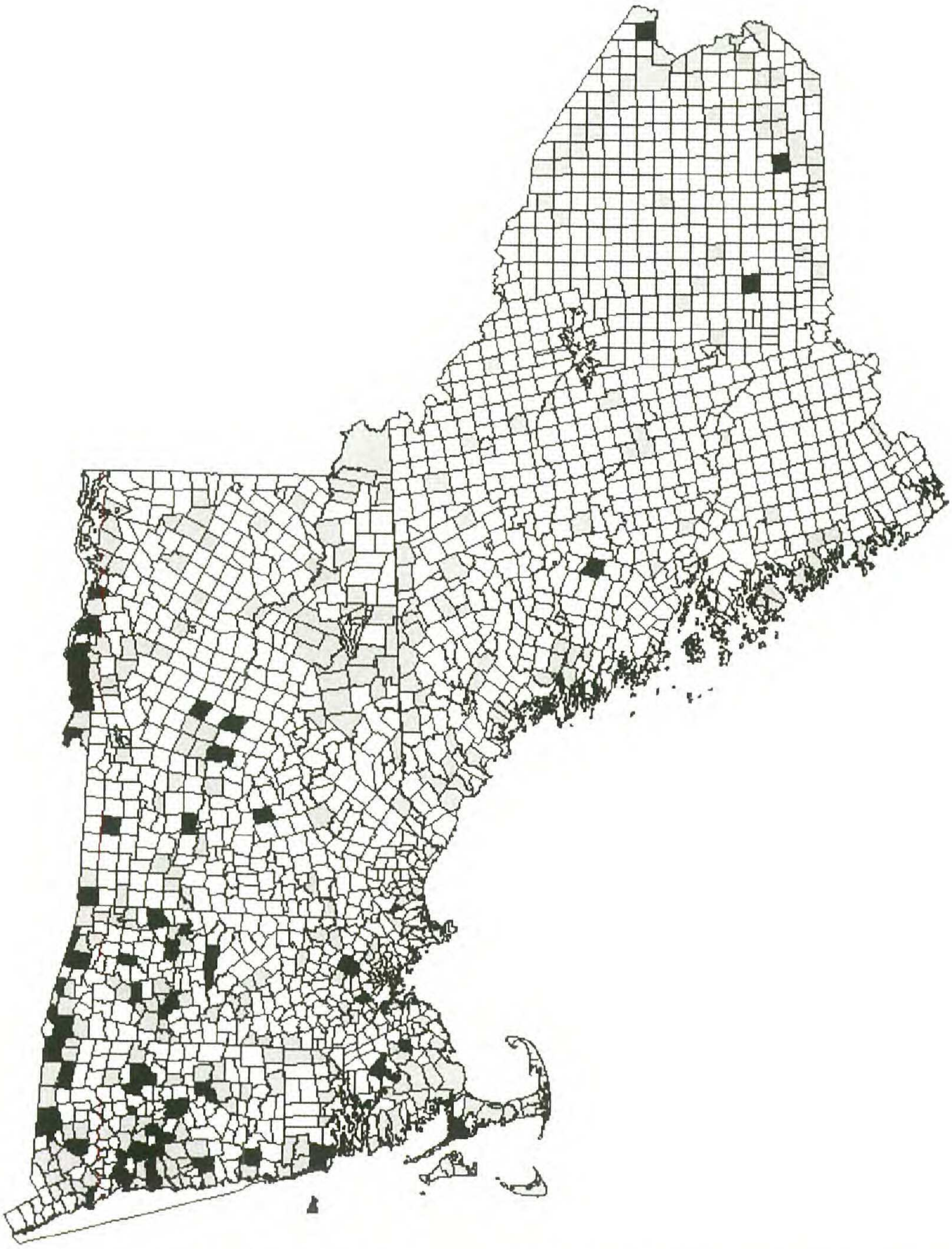

Figure 1. Map of New England states showing town boundaries. Gray fill indicates towns that had one or more occurrences of the rare species covered in the Conservation and Research Plans but had no invasives occurring at rare species stations within the town. Black shading indicates towns in which rare species were recorded as co-occurring with invasive species at particular sites. Towns with no fill had no rare species sites recorded from the Conservation and Research Plans; thus, no co-occurring invasives are recorded for these towns on the map, even though they may very well exist in these towns.

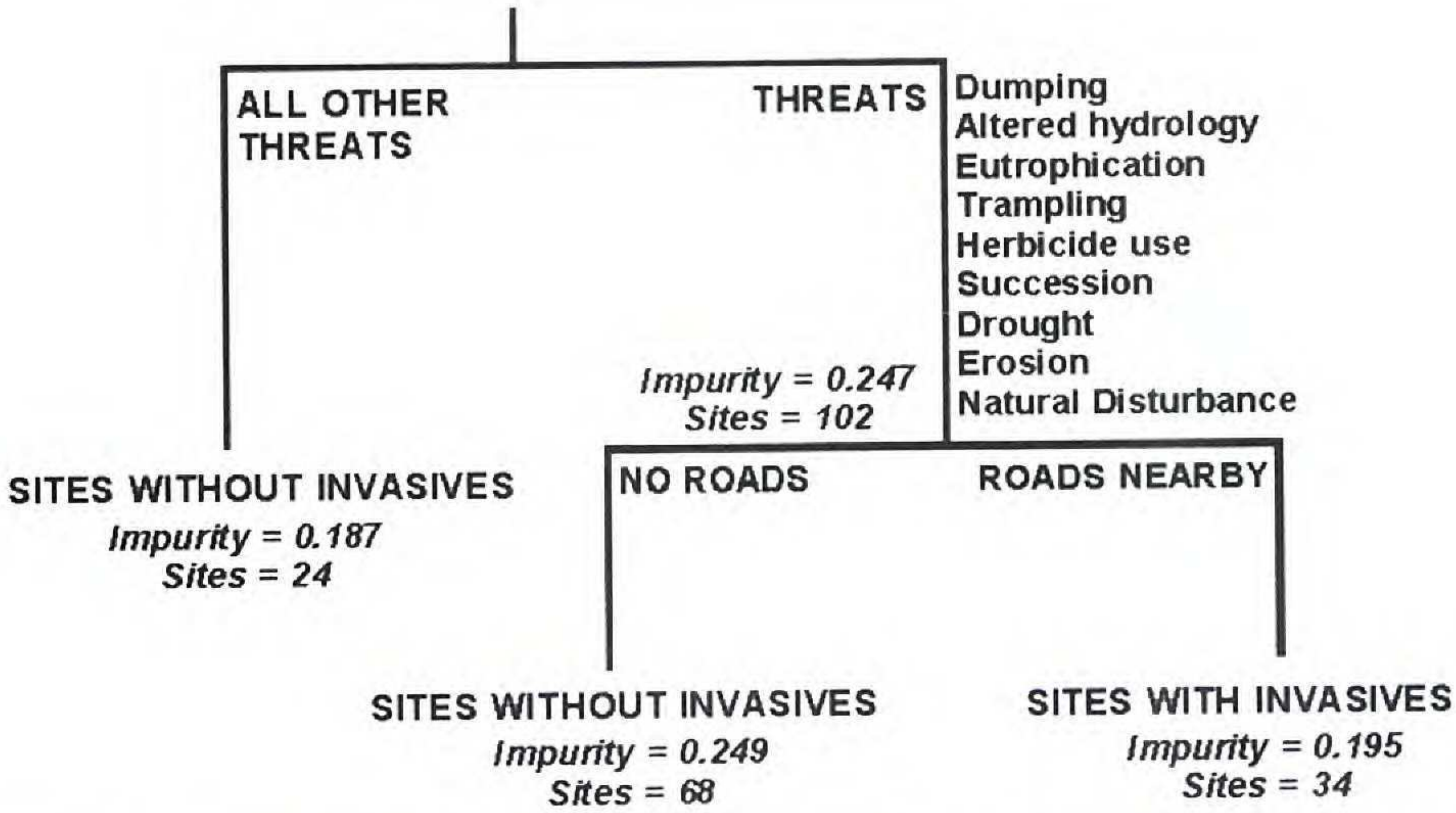

Figure 2. Classification tree on categorical data showing the variable states that best distinguish invaded and non-invaded sites (N = 126 total cases). Each node shows the number of cases (sites) that were split into "uninvaded" and "invaded" categories by each splitting variable; the impurity level at each node is proportional to the number of cases that were misclassified. The first bifurcation occurred on a suite of threats, which are listed at the node. The second bifurcation was on presence or absence of nearby roads. Overall model PRE was 0.109.

threats, invasion probability was higher among those in close proximity to roads (second bifurcation in Figure 2).

Invaded populations also tended to show marginally but not significantly more frequent declines in population numbers ($\chi^2 = 2.78$; df = 1, $P = 0.07$). The mean population size of invaded populations was 706 (±249 SE), approximately half that of uninvaded populations (1423 ± 849), but these differences were not significant by paired *t*-test due to high variance. The overall loss of rare plant populations (EOs) from historical levels (based on herbarium collections) to the present was also compared among species that co-occurred with invasive species and those that did not. Species with invasives suffered a higher proportion of populations lost (56.6% ± 0.04 SE of original populations gone) than uninvaded species (43.1% ± 0.05 of original populations gone), indicating a possible correlative link between prevalence of invasives and local extinctions ($t = 1.959$, $P = 0.054$). However, loss of populations was not correlated significantly with the number of sites invaded per species (by Pearson correlation). Likewise, classification analysis (data not shown; PRE = 0.211) did not separate EOs with declining populations from those showing no decline on the basis of invasion status. Rather, population decline was associated primarily with particular habitat types (specifically, anthropogenic habitats including railroad and power line rights-of-way and old fields) and secondarily with small starting population sizes (< 14 plants per EO).

Classification tree analysis was also used to identify environmental factors associated with species with invasive co-occurrences and species not experiencing invasive threats (Figure 3). Invaded species were more frequently associated with particular types of threats, including mowing, natural disturbance, herbivory, erosion, collection, and eutrophication. Within species that faced additional threats, those occurring in lakes and lake shores, rich woods, and former agricultural sites exhibited lower rates of invasion than those of other habitats. Within the suite of species not associated with additional threats, a higher frequency of invasion was observed in sites under conservation protection than in unprotected areas.

DISCUSSION

Despite half a century of research on the characteristics and impacts of invasive species (Elton 1958), and a broad recognition that invasive species are a leading factor in the endangerment of rare species (Wilcove et al. 1998), we still have few data that specifically document the prevalence of invasive species at rare species sites. Studies that characterize distributions of invasive species at landscape or regional scales are few (Grice et al. 2000; Higgins et al. 1999; Huebner 2003; Kalkhan and Stohlgren 2000; Lockwood et al. 2001; McKinney 2002; Pysek et al. 2002); none have been attempted as yet for New England, and none have addressed multiple rare species. Data collected as part of a comprehensive conservation planning process by the New England Wild Flower Society provide a unique opportunity to quantify the co-occurrence of invasive and rare species and to begin to describe the impact of invasions on listed taxa. Such analyses are critical to justify efforts to regulate activities that contribute to invasive species spread. In order to prioritize management efforts, we also need to understand which invasive species pose the greatest threats, which rare species are most vulnerable, and what environmental factors are associated with invasions (Elias 1987; Hobbs and Humphries 1995).

The data set presented here covers 81 rare plant species for which detailed site observations have occurred. This is a subset, albeit a sizable one, of the total number of rare species listed in New England, and can only imperfectly represent the state of our knowledge about the true distribution of these rare species in the region. Data like these are necessarily somewhat biased by collecting and surveying trends and are artifacts, to a certain extent, of the preferences of botanists for focusing

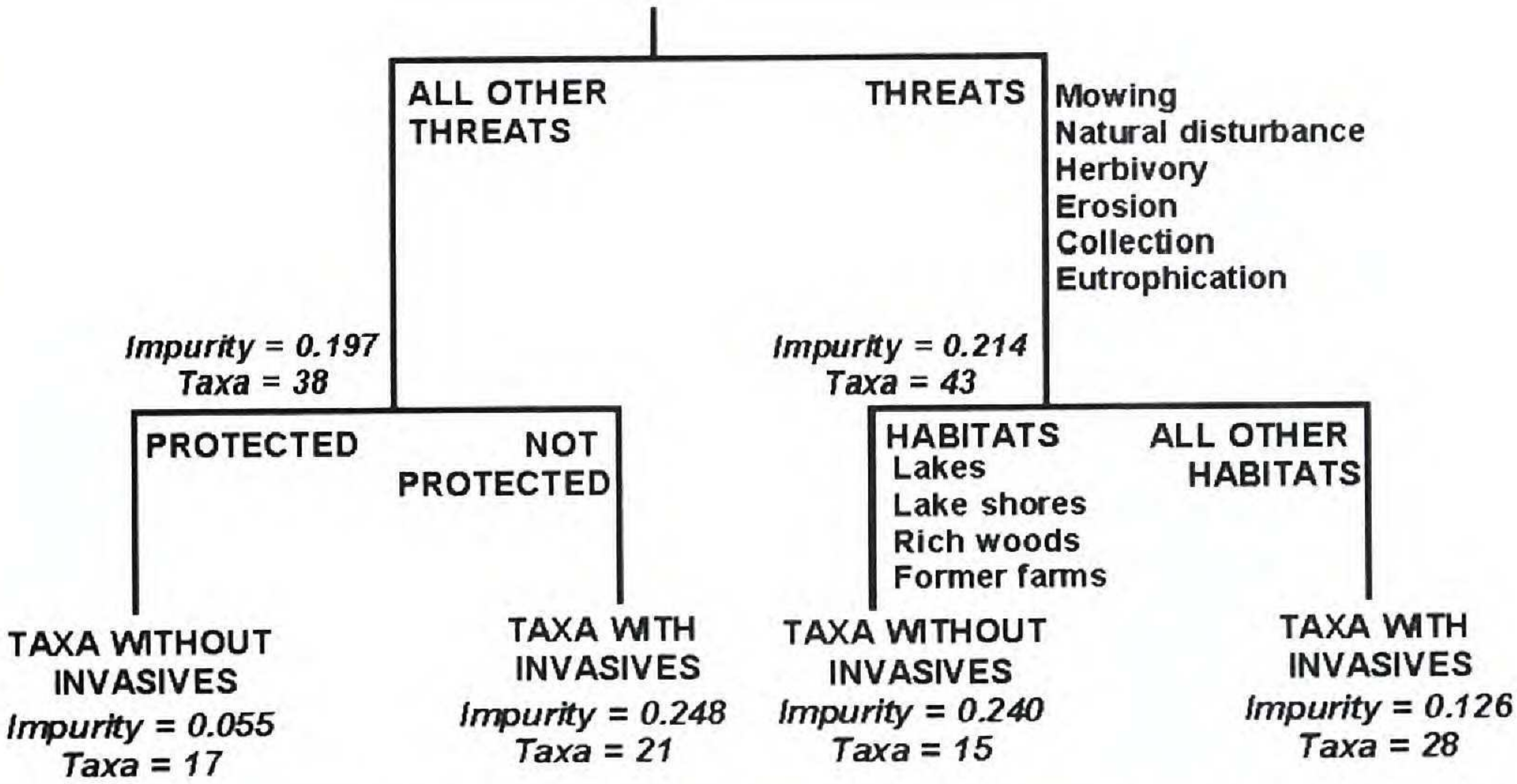

Figure 3. Classification tree showing the variable states that best distinguish species that exhibited co-occurring invasives and those that were free of invasives (N = 81 species). Numbers of taxa at each node show the number of cases that were split into "uninvaded" and "invaded" categories by each splitting variable. The first bifurcation was on the presence of all threats (see text for details). Bifurcations then proceeded on protection status (held or not held by a conservation entity) and habitat type (listed in the figure). Misclassification rates (impurity levels) ranged from 0.055 to 0.248 at each node. Overall model PRE was 0.347.

rare plant searches in particular areas. However, New England is among the most thoroughly botanized regions of North America, and recent efforts both to reverify and collate data from herbarium specimens (the Herbarium Recovery Project of NEPCoP) and to train hundreds of plant surveyors to recognize and document both rare and invasive species (the Plant Conservation Volunteer Program and the Invasive Plant Atlas of New England) have yielded some of the most complete information available for any region on the distribution and status of rare and invasive plant species. The data presented here lay the foundation for future, more targeted surveys to determine which rare plant stations are most vulnerable to invasive species and for long-term studies that document the actual ecological effects of invasives on the viability of rare plant populations. There already exist examples from management-oriented trials in which removal of an invasive species has a demonstrably positive impact on a target rare taxon or natural community (i.e., The Nature Conservancy Wildland Invasive Species Team 2003), including some trials addressing species covered in the NEPCoP Conservation Plans. However, the majority of these trials remain anecdotal or unpublished, and scientific results from adaptive management need to be circulated much more widely. The restoration successes and negative effects of management to remove invasive species from rare species localities should be carefully and critically monitored over a minimum of several years and the findings published and widely disseminated (e.g., Farnsworth and Meyerson 1999b; Manchester and Bullock 2000; Stylinski and Allen 1999).

These analyses demonstrate that invasive plant species co-occur with nearly half (47%) of the 81 rare species studied. This accords in magnitude with large-scale estimates for 1055 state- or federally-listed plant species in the United States, of which 57% were viewed as affected by alien species (Wilcove et al. 1998). For the rare species with reported invasions, an average of more than one-third (37.7%) of their populations had an invasive species present, representing a substantial potential impact on the viability of each of these taxa as a whole in New England. The data suggest that the presence of invasive species may be correlated with both losses of populations (local extinction) and declines in population size. However, declines also tended to reflect larger environmental variables (such as anthropogenic disturbance of habitat) that may themselves simply facilitate colonization by invasive species at the same time as they harm rare species. Much more detailed experimental studies are needed to tease apart the precise impacts of invasive species from a host of complex factors that impinge on population viability. The list of invaded species (Table 1) offers a suite of taxa on which such studies could be focused.

Invasive species co-occurred with rare plants principally along major New England watercourses, including the Connecticut and Housatonic rivers and Lake Champlain (Figure 1). In part, this reflects the geographic distribution of rare species aggregations in New England (e.g., Massachusetts Natural Heritage and Endangered Species Program 2001), but the concentration along rivers represents only a subset of the rare species "hot spots" in the region (Farnsworth 2003). For example, other regional "hot spots" of rarity were relatively free of invasives, including the White Mountains of New Hampshire, interior Maine, and Cape Cod. Such a distribution also reflects the overall species richness of invasive species in western and southern counties of New England (Magee and Ahles 1999), which provide a source pool for new invasions (*sensu* Zobel 1997). The majority of invasive species identified in this study tend to be especially common in floodplains or mesic uplands with rich alluvial soils. Rivers and streams can transport floating seeds directly and can act as corridors for dispersal by animals (Stohlgren et al. 1998). Likewise, changes in hydrology—particularly dampened flooding intensity and frequency—can create artificially stable conditions for invasive species along river shores (Decamps 1993; Galatowitsch et al. 1999).

Invasions at rare plant sites also tended to occur somewhat more frequently in counties with higher richness and density of rare species. A correlation between invasion frequency and local rare species richness accords with emerging hypotheses that species-rich communities may be more vulnerable to invasions than species-poor assemblages (Kalkhan and Stohlgren 2000; Levine 2000; Levine and D'Antonio 1999; Lonsdale 1999; Pysek et al. 2002; Stohlgren et al. 1999; but see Kennedy et al. 2002). In part, this may result from higher availabilities of resources, including water and nutrients, which favor growth of both rare and invasive species (Stohlgren et al. 1999). Disturbances that transiently release resources, such as eutrophication events, also can favor invasions (Burke and Grime 1996; Davis et al. 2000); in fact, eutrophic sites were associated more frequently with invasions in the present study (Figure 2).

I tested the hypothesis that invasions of rare plant species sites might be more frequently associated with certain habitat variables that promote introduction and establishment of alien propagules. Proximity to roads, for example, has been positively correlated with frequency of invasive species because tires and intentional plantings can transport seeds (e.g., Coleman 2003), disturbance from road construction creates colonization sites (e.g., Harrison et al. 2002; Watkins et al. 2003), and road maintenance practices (i.e., salt usage) favor persistence of invasives over non-invasive species (e.g., Richburg et al. 2001; Wilcox 1989). The model presented here did distinguish invaded sites from uninvaded sites on the basis of nearness to a road (Figure 2). Interestingly, proximity to foot trails was not associated with higher rates of invasion, even though people and animals (e.g., deer) can be sources of introduced seeds along these routes (Vellend 2002).

Habitat disturbance was a significant factor distinguishing invaded and uninvaded populations, and invaded and uninvaded species (Figure 2, 3). Ill-timed mowing, natural disturbances, herbivory, erosion, trampling, dumping, and drought were threats commonly associated with invasions. Disturbance has long been viewed as an important driver in invasions of plant communities (Hobbs and Huenneke 1992; Sher and Hyatt 1999). It is of interest that communities with rare species that occupied areas under conservation protection showed a slightly higher proportion of invasions than those of unprotected sites (Figure 3). This may reflect a higher reporting rate of invasions for these sites by managers, or higher rare species richness and invasibility of protected areas; these hypotheses need to be teased apart in future studies.

Invasive species are both agents and symptoms environmental change. This regional analysis has important implications for the management of both rare and invasive species. Three invasive species accounted for 40% of all invasions at rare species sites in New England (Table 2): *Lythrum salicaria*, *Berberis thunbergii*, and *Celastrus orbiculatus*. These taxa should be targeted for more precise, quantitative studies of their distribution and impacts (e.g., Farnsworth and Ellis 2001). Many invasive species are concentrated in southern and western New England, and rare species with more boreal distributions may currently fall at the northern edge of several invasives' ranges. However, new invasions will have to be watched for in remote northern areas, particularly as climatic warming ensues. Management for invasive species will also have to take into account a complex suite of other interacting environmental factors that influence rare species persistence and decline.

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